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Chapter 1

Computational modelling of evolution: ecosystems and language

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Recently, computational modelling became a very important research tool that enables us to study problems that for decades evaded scientific analysis. Evolutionary systems are certainly examples of such problems: they are composed of many units that might reproduce, diffuse, mutate, die, or in some cases for example communicate. These processes might be of some adaptive value, they influence each other and occur on various time scales. That is why such systems are so difficult to study. In this paper we briefly review some computational approaches, as well as our contributions, to the evolution of ecosystems and language. We start from Lotka-Volterra equations and the modelling of simple two-species prey-predator systems. Such systems are canonical example for studying oscillatory behaviour in competitive populations. Then we describe various approaches to study long-term evolution of multi-species ecosystems. We emphasize the need to use models that take into account both ecological and evolutionary processes. Recently we introduced a simple model of this kind, and its behaviour is briefly summarized. In this multi-species prey-predator system, competition of predators for preys and space results in evolutionary cycling. We suggest that such a behaviour of the model might correspond to long-term periodic changes of the biodiversity of the Earth ecosystem as predicted by Raup and Sepkoski. Finally, we address the problem of the emergence and development of language. It is becoming more and more evident that any theory of language origin and development must be consistent with darwinian principles of evolution. Consequently, a number of techniques developed for modelling evolution of complex ecosystems are being applied to the

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problem of language. We briefly review some of these approaches. We also discuss the behaviour of a recently introduced evolutionary version of the naming-game model. In this model communicating agents reach linguistic coherence via a bio-linguistic transition which is due to the coupling of evolutionary and linguistic abilities of agents.

1.1. Introduction

Evolution is a fundamental property of life. It consists of two basic and in a sense opposing ingredients. Mutations and crossing-over are forces that increase variability of organisms and eventually lead to the formation of new brands and species. Against these processes acts selection and due to limited resources only best adapted organisms survive and pass their genetic material to the next generation.

Evolutionary forces are operating since the very early emergence of life. To large extent they shaped the complicated pattern of past and present speciation and extinction processes. Even qualitative understanding of the dynamics that governs these processes is a very challenging problem. Eldredge and Gould[25,95] noted that palaeontological data show that intensity of speciation and extinction processes varied throughout the life history and periods of evolutionary stagnation were interrupted with bursts of activity (punctuated equilibrium). Such a pattern, at least for a physicist, resembles the behaviour of a system at a critical point. Indeed, similarly to critical systems, some palaeontological data can be also described with power laws.[69] Following the work of Bak and Sneppen,[6] a lot of models that try to explain why an Earth ecosystem might be considered as a critical system, were examined.[69] But the quality of palaeontological data does not allow for definitive statements and some alternative interpretations were also proposed. In particular, an interesting conjecture was made by Raup and Sepkoski who suggested that the pattern of bursts of extinctions is actually periodic in time with a period of approximately 26 mln. years.[86] Despite an intensive research it is not clear what a factor could induce such a periodicity, and certainly, it would be desirable to understand the main macroevolutionary characteristics of Earth's ecosystem.

But it is not only intensity of extinction and speciation processes that is of some interest. In the evolution of life one can distinguish several radical changes that had a dramatic consequences and lead to the emergence of new levels of complexity.[61] As examples of such changes Maynard-Smith and Szathmáry list invention of genetic code, transition from Prokaryotes

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to Eukaryotes, or appearance of colonies. Certainly, such changes had a tremendous impact on the evolution and the current state of the Earth's ecosystem. As a last major transition of this kind, Maynard-Smith and Szathmáry mention the emergence of human societies and language. To large extent this transition was induced by cultural interactions. Such interactions when coupled to evolutionary processes lead to the immensely complex system - human society. According to Dawkins,[21] cultural interactions open a new route to the evolution that is no longer restricted to living forms. Examples of such forms, called memes, include songs (not only human), well known sentences and expressions, fashion or architecture styles. As a matter of fact, events listed as major transitions have an interesting feature in common - they created new mechanisms of information transmission. Language certainly enables transmission and storage of very complex cultural information. Its emergence enormously speeded up the information transfer between generations. Before that, for nearly four billion years of life on Earth, the only information that could be used for evolutionary purposes was encoded in the genome. With language vast amount of information can be exchanged between humans and passed on to subsequent generations. Most likely it was the invention of language that enormously speeded up the the evolution of our civilization and made humans in a sense a unique species. Although the emergence and subsequent evolution of language had tremendous influence, this process is still to large extent mysterious and is considered as one of the most difficult problems in science.[17]

Computer modelling seems to be a very promising technique to study complex systems like ecosystems or langauge. In the present paper we briefly review such an approach and present our results in this field. In section 1.2 we briefly discuss population dynamics of simple two-species prey-predator systems and classical approaches in this field based on Lotka-Volterra equations. We also argue that it is desirable to use an alternative approach, the so-called individual based modelling. An example of such a model is described in section 1.3. In this section we discuss results of numerical simulations of the model concerning especially the oscillatory behaviour.

Processes in simple ecosystems with constant number of non-evolvable species (as described in section 1.2) take place on ecological time scale. To describe real, i.e., complex, ecosystems we have to take into account also evolutionary processes, such as speciations or extinctions. Such processes operate on the so-called evolutionary time scale. Such a time scale

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was usually regarded as much longer than ecological time scale, however, there is a number of examples that show that they are comparable.[28,107] In section 1.4 we briefly review models used to study complex ecosystems. In particular, we emphasize the need to construct models that would take into account both ecological and evolutionary processes. In section 1.5 we examine one of such models which is a multi-species generalization of prey-predator model studied in section 1.3. Investigating extinction of species we show that their intensity changes periodically in time. The period of such oscillations is set by the mutation rate of the model. Since evolutionary changes are rather slow, we expect that such oscillations in the real ecosystem would have very long periodicity. We suggest that such a behaviour agrees with the conjecture of Raup and Sepkoski, but more detailed analysis of the predictions of our model would be desirable. In the final part of this section we suggest that our model might provide an insight into a much different problem. Namely, we attempt to explain the uniqueness of the coding mechanism of living cells as contrasted with the multispecies structure of present-day ecosystems. Apparently, at the early stage of life a primitive replicator happened to invent the universal code that was so effective that it spread over the entire ecosystem. However, at a certain point such a single-species ecosystem become unstable and was replaced by a multi-species ecosystem. In our model, upon changing a control parameter, a similar transition (between single- and multi-species ecosystems) takes place and we argue that it might be analogous to the early-life transition.

In section 1.6 we review computational studies on language evolution. An important class of models is based on the so-called naming game introduced by Steels.[101] Recently, we examined an evolutionary version of this model and showed that coupling of evolutionary and linguistic interactions leads to some interesting effects.[55] Namely, for sufficiently large intensity of linguistic interactions, there appears an evolutionary pressure that rapidly increases linguistic abilities and the model undergoes an abrupt bio-linguistic transition. In such a way communicating agents establish a common vocabulary and the model reaches the so-called linguistic coherence. Our model incorporates both learning and evolution. Interaction of these two factors, known as a Baldwin effect,[7] is recently intensively studied also in the context of language evolution.[115] Discussion of the Baldwin effect and related properties in our model is also presented in Section 1.6. We conclude in Section 1.7.

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1.2. Coarse-grained versus individual-based modelling of an ecosystem

Population dynamics provides the basis of the modelling of the ecosystem. Pierre Verhulst, regarded as its founding father, noticed that due to the finite environmental capacity the unlimited growth of the population predicted by the linear growth equation is unrealistic. Consequently, Verhulst proposed that the time evolution of the population should be described by the following equation[112]

$$\frac{dx}{dt} = kx(1 - x/x_M) \tag{1.1}$$

where k is the growth rate, x is the size of the population, and x_M is the environmental capacity. Equation (1.1), that is called logistic equation, found numerous applications in demographic studies. However, to describe any realistic ecosystem one should consider more, possibly interacting, populations. A step in this direction was made by Lotka who examined a simple autocatalytic reaction model.[58] His work was followed by Volterra who wrote down essentially the same set of ordinary differential equations (ODE) studying the statistics of fish catches.[113] Lotka-Volterra equations for two interacting populations of preys (x) and predators (y) can be written as

$$\frac{dx}{dt} = x(a_1 - a_2 y)$$
$$\frac{dy}{dt} = y(-a_3 + a_4 x) \tag{1.2}$$

where a_1, a_2, a_3, and a_4 are some positive constants. Although eqs. (1.2) constitute the canonical model to study periodic oscillations in competitive systems,[66] they were also criticized on various grounds. For example their solution depends on the initial condition, and the very form of eqs. (1.2) is structurally unstable. It means that their small modification (with e.g., higher order terms like $x^2 y$) will typically destroy oscillatory behaviour. Although there are some ODE models where such a limit cycle behaviour is more stable,[60] an important feature of any realistic system is missing in eqs. (1.1) or (1.2). Namely, they neglect spatial heterogenities. The simplest way to take them into account would be to consider x and y as spatially dependent quantities and then to replace eqs. (1.1) or (1.2) with their partial differential analogs. After such a modification eq. (1.1) becomes the famous Fisher equation, that in the one-dimensional case has

the form

$$\frac{dx}{dt} = kx(1 - x/x_M) + D\frac{\partial^2 x}{\partial l^2} \qquad (1.3)$$

where l is the spatial coordinate, D is the diffusion constant and $x = x(t, l)$ depends on t and l. Various extensions of (1.3), that are called sometime reaction-diffusion models, were also intensively studied in ecological contexts.[40,66]

Although description in terms of partial differential equations takes into account some of spatial heterogenities, it is still based on the coarse-grained quantities like $x(t, l)$ and that means that it is essentially of the mean-field nature. Moreover, kinetic coefficients (k, D, x_M, a_1, a_2, a_3, $a_4, \ldots$) that enter such equations are usually difficult to determine from ecological data. Similar problems appear in alternative approaches to spatially extended ecological models based on coupled-map lattices[36] or integrodifference equations.[35] It is thus worth to pursue an alternative approach, the so-called individual based modelling, where to some extent stochastic rules, mimicking realistic processes like death, breeding or movement, are formulated at the level of individual organisms. Models of ecosystems formulated within such an approach are particularly suited for numerical computations and resemble some nonequilibrium statistical mechanics models. Such a similarity is very valuable since the behaviour of ecological systems can be put in a wider perspective.

1.3. Lattice prey-predator models

To simplify calculations individual-based models of prey-predator systems are usually formulated on a cartesian d-dimensional lattice of the linear size N. One can define dynamics of such models in various ways, but to provide a detailed example we present rules used in some of our previous works.[49,53] In our model on each site i of a lattice there is a four-state variable $\epsilon_i = 0, 1, 2, 3$ which corresponds to the site being empty ($\epsilon_i = 0$), occupied by a prey ($\epsilon_i = 1$), occupied by a predator ($\epsilon_i = 2$) or occupied by a prey and a predator ($\epsilon_i = 3$). Its dynamics has one control parameter r ($0 \leq r \leq 1$) and is specified as follows:
- Choose a site at random.
- With the probability r update a prey at the chosen site, provided that there is one (i.e., $\epsilon = 1$ or 3); otherwise do nothing. Provided that at least one neighbor of the chosen site is not occupied by a prey (i.e., $\epsilon = 0$ or 2), the prey (which is to be updated) produces

one offspring and places it on the empty neighboring site (if there are more empty sites, one of them is chosen randomly). Otherwise (i.e., when there is a prey on each neighboring site) the prey does not breed (due to overcrowding).

- With the probability $1 - r$ update a predator at the chosen site, provided that there is one (i.e., $\epsilon = 2$ or 3). Provided that the chosen site is occupied by a predator but is not occupied by a prey ($\epsilon = 2$), the predator dies (of hunger). If there is a prey on that site (i.e., $\epsilon = 3$), the predator survives and consumes the prey from the site it occupies. If there is at least one neighboring site which is not occupied by a predator, the predator produces one offspring and places it on the empty site (chosen randomly when there are more such sites).

As neighboring sites, i.e., sites where offsprings can be placed, we usually consider the nearest neighbours, but taking into account further neighbours does not change the results qualitatively.[47] To characterize the behaviour of the model let us introduce the densities of preys (x) and predators (y) defined as

$$x = \frac{1}{N^d} \sum_i (\delta_{\epsilon_i,1} + \delta_{\epsilon_i,3}), \quad y = \frac{1}{N^d} \sum_i (\delta_{\epsilon_i,2} + \delta_{\epsilon_i,3}), \qquad (1.4)$$

where summation is over all N^d sites i and δ is Kroneckers δ-function. Of the main interest are actually averages $\langle x \rangle$ and $\langle y \rangle$, where averaging is over simulation time.

From the above rules it follows that the model has two absorbing states (i.e., once the model enter such a state it remains trapped there for ever). The first one is filled with preys only ($x = 1$, $y = 0$) and the second one is empty ($x = 0$, $y = 0$). Simulations[47,49,53] show that for large enough r, both populations coexist and the model is in the active phase ($x > 0$, $y > 0$). When the update rate of preys r decreases, their number becomes to small to support predators. For sufficiently small r predators die out and the model quickly reaches the absorbing state where it is filled with preys (the empty absorbing state has a negligible probability of being reached by the model dynamics). The phase transition between active and absorbing phase was observed at positive r for $d = 1, 2$ and 3. At least for $d = 1$ (linear chain) Monte Carlo simulations clearly show that the phase transition belongs to the directed percolation (DP) universality class[53] (see Fig. 1.1).

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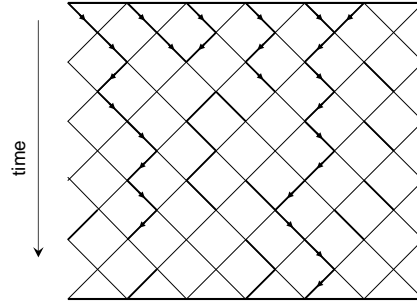

Fig. 1.1.   In the directed percolation problem a fraction of bonds on a lattice is perme-
able (thick lines). From the top horizontal line water starts to flow downward through
permeable bonds. Bonds that are reachable by water are shown with arrows. If at a cer-
tain (horizontal) level there would be no water, there would be no water below that level
(absorbing state). When concentration of permeable bonds exceeds a certain threshold
value a cluster of permeable bonds that spans from top to bottom is formed. At the
threshold value the model is critical. A lot of dynamical models with a single absorbing
state belong to the directed percolation universality class

Such a behaviour is not surprising. There are by now convincing nu-
merical and analytical arguments that various models possessing a single
absorbing state generically belong to the DP universality class.[37] Moreover,
models with multiple, but asymmetric absorbing states (such as e.g., the
model analysed in this section) also belong to this universality class (mod-
els with multiple but symmetric absorbing states typically belong to some
other universality classes, or undergo discontinuous phase transitions[52]).
However, studying the critical behaviour of models with absorbing-state
phase transitions is not entirely straightforward. For finite systems (which
is obviously the case in various simulational techniques) and close to the
critical point, the model has a non-negligible probability of entering an ab-
sorbing state even when control parameters are such that the infinite system
would remain in the active phase. Such a behaviour sets a size-dependent
timescale (i.e., the lifetime of the active state) that severely affects sim-
ulations. A special technique, the so-called dynamical Monte Carlo, is
needed to obtain precise estimation of critical exponents for models of this
kind.[32,37]

Of our main interest, however, is the oscillatory behaviour of the model.
To examine it, we measured the variances of the densities x and y as well as
their Fourier transforms. Simulations show that for $d = 1$ and $d = 2$ in the

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limit $N \to \infty$ stochastic fluctuations wash out the oscillatory behaviour and the variances of densities vanish. However, for $d = 3$ in the active phase and close to the absorbing transition, there is a range of r where oscillatory behaviour survives in the limit $N \to \infty$.[a] Oscillations occur essentially for any initial conditions and their period only weakly depends on the parameter r.

It is the dimension of the lattice d that most likely plays an important role. Indeed, simulations show that for $d = 2$ models but with larger number of neighbouring sites oscillations are again washed out in the limit $N \to \infty$.[47] Such a result is in agreement with some arguments of Grinstein *et al.*[33] who related temporal periodic phases of noisy extended systems and smooth interfaces in growth models and concluded that oscillations might exist but only for $d > d_c = 2$. The (r, d) phase diagram of our model is sketched in Fig.1.2.

To get an additional insight into the behaviour of the model we can write mean-field equations that describe the time evolution of the densities x and y. Simple arguments[49] lead to the following set of equations

$$\frac{dx}{dt} = rx(1 - x^w) - (1 - r)xy$$
$$\frac{dy}{dt} = (1 - r)xy(1 - y^w) - (1 - r)y(1 - x) \qquad (1.5)$$

where w is the number of neighboring sites, as defined in the dynamical rules of the model (in most of our simulations neighbouring sites were nearest neighbours and in such a case $w = 2d$). For example in the first equation of (1.5), the first term $(rx(1 - x^w))$ describes the growth rate of preys due to updating a site with prey (rx) that happen to have at least one empty neighbouring site $((1 - x^w))$. The second term $((1 - r)xy)$ describes the decrease rate of preys due to an update of a site that happened to be a predator and that is also occupied by a prey. However, predictions of approximation (1.5) even qualitatively disagree with numerical simulations. In particular, in any dimension d the approximation (1.5) predicts that for any positive r there is no phase transition between active and absorbing phases. Moreover, within this approach there is no indication of the oscillatory phase, as observed in Monte Carlo simulations for $d = 3$.

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[a]Such a conclusion is based on the non-vanishing of variances of densities in this limit. Strictly speaking, based solely on such a behaviour, one cannot exclude that this is e.g., chaotic behaviour that sets in. However, a pronounced peak in the Fourier transform of the time-dependent densities strongly supports the oscillatory interpretation of the numerical data.

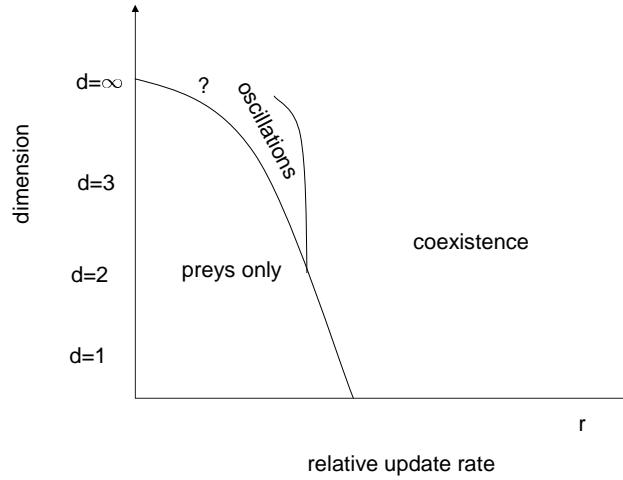10   *A. Lipowski and D. Lipowska*

Fig. 1.2.   The schematic phase diagram of the lattice prey-predator model. The phase transition separating preys-only and coexistence phases most likely belongs to the directed percolation universality class,[53] but in more general models other transitions are possible.[63] It is not clear what is the fate of the oscillatory phase in $d > 3$ case, since the mean-field equations (1.5) (that most likely correctly describe the model in large dimension) do not predict the oscillatory regime.

In the approximation (1.5) the probability that a site is occupied by a prey and predator is given as xy. This is of course only an approximation, and a much better scheme is obtained where this probability is considered as yet another variable (z), whose evolution follows from the dynamical rules of the model. In such a way we arrive at the following set of equations[47]

$$\frac{dx}{dt} = rx(1 - x^w) - (1 - r)z$$
$$\frac{dy}{dt} = (1 - r)z(1 - y^w) - (1 - r)(y - z) \qquad (1.6)$$
$$\frac{dz}{dt} = \frac{rx(1 - x^w)(y - z)}{1 - x} - \frac{(1 - r)z(1 + z - x - y)(1 - y^w)}{1 - y} - (1 - r)zy^w$$

In the first term of the third equation of Eqs. (1.6) $x(1 - x^w)$ gives the probability that the chosen site contains the prey and at least one of its neighbours does not. The factor $\frac{y-z}{1-x}$ gives the probability that the site chosen for reproduction of the prey is occupied by the predator only. The

set of equations (1.6) remains in a much better (than (1.5)) agreement with Monte Carlo simulations.[48] In particular it predicts, oscillatory regime for $w \geq 4$. In Monte Carlo simulations of models on cartesian lattices (we made simulations only for $d = 1, 2, 3$) oscillations appear only in the $d = 3$ case (i.e., $w = 6$), and for $d = 2$ (i.e., $w = 4$) these were only quasi-oscillations with the amplitude that vanishes in the limit $N \to \infty$.

It is interesting to ask what is the mechanism that triggers the emergence of finite-amplitude oscillations. Rosenfeld *et al.* suggested[64,88] that oscillatory behaviour in another lattice prey-predator model is induced by some kind of percolation transition (see Fig. 1.3). However, precise measurements of cluster properties in our model has shown that although some percolation transitions are indeed close to the onset of oscillatory regime, they clearly do not overlap with this onset.[48] Another proposal relates oscillations with some kind of stochastic resonance.[49,84] Such a relation might be suggested by the mean-field approximation (1.5) that in fact describes a quasi-oscillatory dynamical system. Stochastic fluctuations, that are present in the lattice model but are neglected in the mean-field description, might be considered as a noise perturbing such a dynamical system. As shown by Gang et al.[29] due to stochastic resonance, in some low-dimensional autonomous dynamical systems noise might induce oscillatory behaviour and one can expect that a similar scenario operates in lattice prey-predator systems.

There are also other lattice prey-predator models were similar oscillations were observed.[5,10,59,78,83,90] In a more general model, were predation and reproduction time scales are independent, a first-order phase transition might appear.[63] One can also mention that there are some important ecological problem that so far were not examined with individual based modelling but where such an approach might prove to be valuable. In this context one can mention various synchronization problems in spatially extended ecological systems[9] and in particular the Moran effect describing synchronization of populations exposed to common noise.[26]

1.4. Modelling of complex ecosystems

Models that we discussed in the previous section describe rather simple ecosystems composed of few (two, three,...) species. Dynamics of such models implements basic ecological processes: reproduction, death, and in some cases also migration or aging. In such models changes of the populations takes place on a characteristic ecological time scale that is set by the
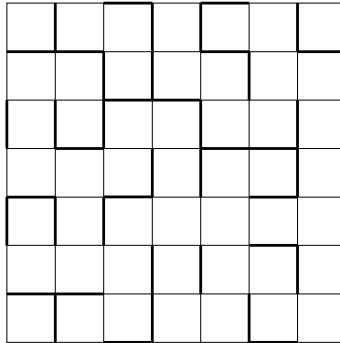
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Fig. 1.3. In the bond percolation problem a fraction c of bonds is occupied (thick lines).[92,93] Neighbouring occupied bonds form clusters. When c exceeds a certain threshold value an infinite (i.e., spanning the entire lattice) cluster is formed. In a related problem of site percolation a fraction of sites is occupied and neighbouring occupied sites form clusters. As suggested by Rosenfeld *et al.*[64,88] oscillatory behaviour might be induced by some kind of percolation transition i.e., formation of an infinite cluster of preys or predators. Although the idea is appealing some calculations do not support it.[48]

dynamics of the models Typically, in real ecosystems this scale is of the order of years (for example, in a hare-lynx system oscillations with the period of approximately 10 years were identified[91]). But there are also some other than ecological processes. On the so-called evolutionary (or geological) time scale the entire species might die, change, or give rise to a new species. The evolutionary time scale is usually considered as much longer than ecological one.[30] As a result very often researchers constructed specific models directed toward either ecological or evolutionary processes. However, there are numerous examples showing that these time scales are not that much different and in some cases they are even comparable.[28,107] Thus, such a separation of time scales is to some extent artificial and was used mainly for the ease of modelling (for a theoretical discussion of some related issues see e.g., the paper by Khibnik and Kondrashov[43]). Actually, the complexity of real multi-species ecosystems and the difficulty to model them to some extent follow from the fact that these scales are not completely separated and ecological and evolutionary processes affect each other.

A model of multi-species ecosystem that tries to describe evolutionary processes and drew considerable attention especially in physicists community was introduced by Bak and Sneppen[6] (see Fig. 1.4). An interesting property of this model is its self-organized criticality. Namely, dynamics

drives the model into the state where extinctions are strongly correlated (like in critical systems) and such a behaviour resembles the punctuated equilibrium hypothesis of Eldredge and Gould.[25,95]   However, the Bak-Sneppen model has the dynamics that is operating at the level of species and refers to the (still controversial) notion of fitness. Thus, the model neglects ecological effects and despite rich and intriguing dynamics can be considered only as a toy model of an ecosystem. Nevertheless, the work of Bak and Sneppen inspired other researchers to examine a number of models with species-level dynamics. For example, Vandevalle and Ausloos incorporated speciation,[110] Solé and Manrubia introduced various interactions between species,[98] and Amaral and Meyer considered some elements of the food-chain dynamics.[4] Although these models drastically simplify the dynamics of real ecosystems they do provide a valuable qualitative description of some complex problems such as formation of trophic levels or correl
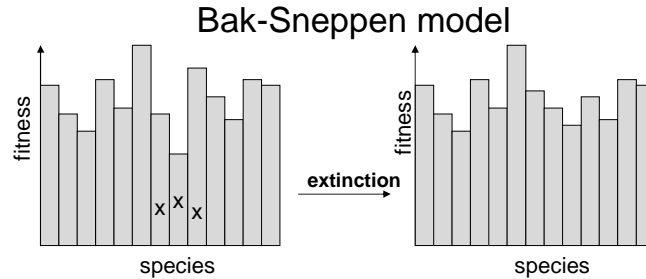

Fig. 1.4.   The one-dimensional version of the Bak-Sneppen model. First, the species of lowest fitness is selected. Then this species and two of its neighbours (denoted by crosses) go extinct and are replaced by three new species with randomly selected fitness. Such a simple dynamics (no control parameters) drives the model into the critical state. The extremal dynamics of the Bak-Sneppen model was criticized on biological grounds, nevertheless this model drew considerable attention and is one of the main models of the self-organized criticality.

Recently, computational methods made feasible the analysis of models that incorporate both ecology and evolution. One way to construct such models is to generalize Lotka-Volterra equations to the multi-species case and to implement some speciation and extinction mechanism. Such an approach has already been developed,[2,12,18] but it has similar drawbacks as original Lotka-Volterra model, namely it neglects spatial heterogeneities. In an alternative approach one uses individual-based dynamics and some

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models of multi-species ecosystems equipped with such a dynamics were examined.[15] A diagram that illustrates some types of models and their range of applicability is shown in Fig.1.5.
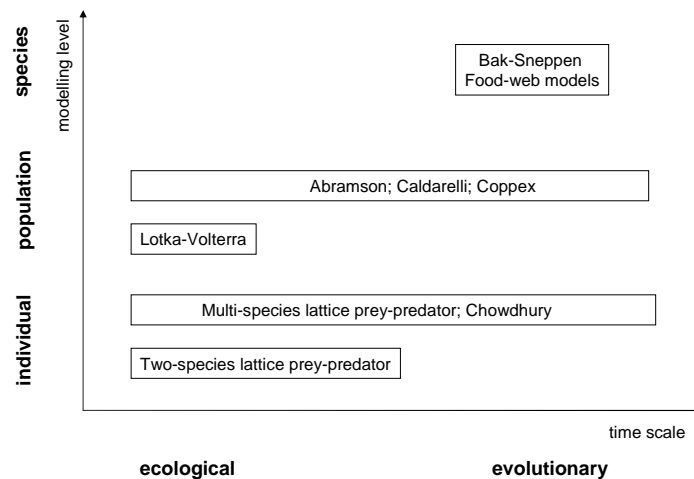

Fig. 1.5.   Ecological and evolutionary aspects of the modelling of an ecosystem. The most coarse-grained models of ecosystem have dynamics operating at the level of species. Such models (e.g., Bak-Sneppen,[6] Food-web models[4]) neglect population level processes and describe ecosystem at the evolutionary time scale. Models originating from the Lotka-Volterra model use dynamics defined at the population level. Such models describe ecological processes in few-species ecosystems, but multi-species versions of Abramson,[2] Caldarelli et al.,[12] or Coppex et al.,[18] that encompass also the evolutionary process were examined as well. Similar range of applicability have models with individual level dynamics (the model of Chowdhury et al.[15] neglects, however, the heterogeneities in spatial distribution of organisms).

1.5. Multispecies prey-predator model and periodicity of extinctions

In this section we describe the multi-species version of a lattice prey-predator model.[51,54] Numerical simulations of the model show that the

periodicity of mass extinctions, that was suggested by Raup and Sepkoski,[86] might be a natural feature of the ecosystem's dynamics and not the result of a periodic external perturbation.

1.5.1. *Model*

Our model might be considered as a generalization of the two-species model described in section 1.3. The model is defined on a d-dimensional cartesian lattice of the linear size N. Similarly to the two-species model one uses the four-state variables $\epsilon_i = 0, 1, 2$ or 3. In addition, each predator is characterized by its size m ($0 < m < 1$) that determines its consumption rate and at the same time its strength when it competes with other predators. Only approximately the size m can be considered as related with physical size. Predators and preys evolve according to rules typical to such systems (e.g., predators must eat preys to survive, preys and predators can breed provided that there is an empty site nearby, etc.). In addition, the relative update rate for preys and predators is specified by the parameter r ($0 < r < 1$) and during breeding mutations are taking place with the probability p_{mut}. More detailed definition of the model dynamics is given below:

- Choose a site at random (the chosen site is denoted by i).
- Provided that i is occupied by a prey (i.e., if $\epsilon_i = 1$ or $\epsilon_i = 3$) update the prey with the probability r. If at least one neighbor (say j) of the chosen site is not occupied by a prey (i.e., $\epsilon_j = 0$ or $\epsilon_j = 2$), the prey at the site i produces an offspring and places it on an empty neighboring site (if there are more empty sites, one of them is chosen randomly). Otherwise (i.e., if there are no empty sites) the prey does not breed.
- Provided that i is occupied by a predator (i.e., $\epsilon_i = 2$ or $\epsilon_i = 3$) update the predator with the probability $(1-r)m_i$, where m_i is the size of the predator at site i. If the chosen site i is occupied by a predator only ($\epsilon_i = 2$), it dies, i.e., the site becomes empty ($\epsilon_i = 0$). If there is also a prey there ($\epsilon_i = 3$), the predator consumes the prey (i.e., ϵ_i is set to 2) and if possible, it places an offspring at an empty neighboring site. For a predator of the size m_i it is possible to place an offspring at the site j provided that j is not occupied by a predator ($\epsilon_j = 0$ or $\epsilon_j = 1$) or is occupied by a predator ($\epsilon_j = 2$ or $\epsilon_j = 3$) but of a smaller size than m_i (in such a case the smaller-size predator is replaced by an offspring of the larger-size predator).

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> The offspring inherits its parent's size with the probability $1 - p_{mut}$
> and with the probability p_{mut} it gets a new size that is drawn from
> a uniform distribution.

At first sight one can think that such a model describes an ecosystem
with two trophic levels (preys and predators) and only with predators be-
ing equipped with evolutionary abilities, which would be of course highly
unrealistic. Let us notice, however, that expansion of predators sometimes
proceeds at the expense of smaller-size predators. Thus, predators them-
selves are involved in prey-predator-like interactions. Perhaps it would be
more appropriate to consider unmutable preys as a renewable (at a finite
rate) source of, e.g., energy, and predators as actual species involved in var-
ious prey-predator interactions and equipped with evolutionary abilities.

In the remaining part of this section we will describe a possible appli-
cation of our model to the problem of mass extinctions and to the problem
of multiplicity of species in the Earth ecosystem as contrasted with the
uniqueness of the genetic code.

1.5.2. *Extinctions*

The suggestion that mass extinctions might be periodic in time was made
by Raup and Sepkoski.[86] While analyzing fossil data, they noticed that
during the last 250 My (million years) mass extinctions on Earth appeared
more or less cyclically with a period of approximately 26My. Although their
analysis was initially questioned,[77] some other works confirmed Raup and
Sepkoski's hypothesis.[27,81,82] The suggested large periodicity of mass ex-
tinctions turned out to be very difficult to explain. Indeed, 26My does not
seem to match any of known Earth cycles and some researchers have been
looking for more exotic explanations involving astronomical effects,[20,85] in-
creased volcanic activity,[104] or the Earth's magnetic field reversal.[103] So
far, however, none of these proposals has been confirmed. One should also
note that the most recent analysis of palaeontological data that span last
542My strongly supports the periodicity of mass extinctions albeit with a
larger cycle of about 62My.[87]

Lacking a firm evidence of an exogenous cause, one can ask whether
the periodicity of extinctions might be explained without referring to such
a factor. In sections 1.2 and 1.3 we already mentioned that periodic be-
haviour of some prey-predator systems is not the result of periodic driving
but rather a natural feature of their dynamics. However, the period of

oscillations in such systems is determined by the growth and death rate coefficients of interacting species and is of the order of a few years rather than tens of millions. Consequently, if the periodicity of mass extinctions is to be explained within a model of interacting species, a different mechanism that generates long-period oscillations must be at work.

Such a mechanism might be at work in the multi-species model described in section 1.5.1. Numerical simulations[51,54] show that the model generates long-period evolutionary oscillations The period of these oscillations is determined by the inverse of the mutation rate and we argued that it should be several orders of magnitude longer than in the Lotka-Volterra oscillations. The mechanism that generates oscillations in our model can be briefly described as follows: A coevolution of predator species induced by the competition for food and space causes a gradual increase of their size. However, such an increase leads to the overpopulation of large predators and a shortage of preys. It is then followed by a depletion of large species and a subsequent return to the multi- species stage with mainly small species that again gradually increase their size and the cycle repeats. Numerical calculations for our model show that the longevity of a species depends on the evolutionary stage at which the species is created. A similar pattern has been observed in some palaeontological data[62] and, to our knowledge, the presented model is the first one that reproduces such a dependence. Let us notice that the oscillatory behaviour in a prey-predator system that was also attributed to the coevolution has been already examined by Dieckmann et al.[24] In their model, however, the number of species is kept constant and it cannot be applied to study extinctions. Moreover, the idea that an internal ecosystem dynamics might be partially responsible for the long-term periodicity in the fossil records was suggested by Stanley[100] and later examined by Plotnick and McKinney.[80] However, according to Stanley mass extinctions are triggered by external impacts. Their approximately equidistant separation is the result of a delayed recovery of the ecosystem. In our approach no external factor is needed to trigger such extinctions and sustain their approximate periodicity.

A gradual increase of size of species in our model recalls the Cope's rule that states that species tend to increase body size over geological time. This rule is not commonly accepted among paleontologists and evolutionists and was questioned on various grounds.[99] However, recent studies of fossil records of mammal species are consistent with this rule.[3,111] Perhaps our model could suggests a way to obtain a theoretical justification of this rule.

Although very complicated, in principle, it should be possible to es-

timate the value of the mutation probability p_{mut} from the mutational properties of living species. Let us notice that in our model mutations produce an individual that might be substantially different from its parent. In Nature, this is typically the result of many cumulative mutations and thus we expect that p_{mut} is indeed a very small quantity. Actually, p_{mut} should be considered rather as a parameter related with the speed of morphological and speciation processes that are known to be typically very slow.[30] Perhaps a different version of the mutation mechanism where a new species would be only a small modification of its parental species could be more suitable for comparison with living species, but it might require longer calculations.

1.5.3. *Unique genetic code and the emergence of a multi-species ecosystem*

All living cells use the same code that is responsible for the transcription of information from DNA to proteins.[75,106] It suggests that at a certain point of evolution of life on Earth a replicator that invented this apparently effective mechanism was able to eliminate replicators of all other species (if they existed) and establish, at least for a short time, a single-species ecosystem. Although this process is still to a large extent mysterious, one expects that subsequent evolution of these successful replicators leads to their differentiation and proliferation of species. In such a way the ecosystem shifted from a single- to multi-species one.[50] It seems to us that our model might provide some insight into this problem. Numerical simulations show[51,54] that the oscillatory behaviour appears in our model only for the relative update rate $r < 0.27$. When preys reproduce faster ($r > 0.27$), a different behaviour can be seen and the model reaches a steady state with almost all predators belonging to the same species with the size m close to 1. Only from time to time a new species is created with even larger m and a change of the dominant species might take place. In our opinion, it is possible that at the very early period of evolution of life on Earth, the ecosystem resembled the case $r > 0.27$. This is because at that time substrates ('preys') were renewable faster than primitive replicators ('predators') could use them. If so, every invention of the increase of the efficiency ('size') could invade the entire system. In particular, the invention of the coding mechanism could spread over the entire system. A further evolution increased the efficiency of predators and that effectively shifted the (single-species) ecosystem toward the $r < 0.27$ (multi-species, oscillatory) regime.

1.5.4. *Multispecies prey-predator model - summary and per-spectives*

In this section we discussed a model where densities of preys and predators as well as the number of species show long-term oscillations, even though the dynamics of the model is not exposed to any external periodic forcing. It suggests that the oscillatory behaviour of the Earth ecosystem predicted by Raup and Sepkoski could be simply a natural feature of its dynamics and not the result of an external factor. Some predictions of our model such as the lifetime of species or the time dependence of their population sizes might be testable against palaeontological data. Certainly, our model is based on some restrictive assumptions that drastically simplify the complexity of the real ecosystem. Nevertheless, it includes some of its important ingredients: replication, mutation, and competition for resources (food and space). As an outcome, the model shows that typically there is no equilibrium-like solution and the ecosystem remains in an evolutionary cycle. The model does not include geographical barriers but let us notice that palaeontological data that suggest the periodicity of mass extinctions are based only on marine fossils.[87] More realistic versions should take into account additional trophic levels, gradual mutations, or sexual reproduction. One should also notice that the palaeontological data are mainly at a genus, and not species level. It would be desirable to check whether the behaviour of our model is in some sense generic or it is merely a consequence of its specific assumptions. An interesting possibility in this respect could be to recast our model in terms of Lotka-Volterra like equations and use the methodology of adaptive dynamics developed by Dieckmann et al.[24] Of course, the real ecosystem was and is exposed to a number of external factors such impacts of astronomical objects, volcanism or climate changes. Certainly, they affect the dynamics of an ecosystem and contribute to the stochasticity of fossil data. Filtering out these factors and checking whether the main evolutionary rhythm is indeed set by the ecosystem itself, as suggested in the present paper, is certainly a difficult task but maybe worth an effort.

1.6. **Computational approaches to the evolution of language**

In this section we describe computational approaches to the problem of evolution of language. In this field the mainstream research takes the darwinian standpoint: natural selection guided the language development and

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emergence of its basic features. One thus accept that at least some features of language have certain adaptive value and their gradual development is much more plausible than a catastrophic change. There are, however, some issues that still remain unclear within such a darwinian approach. For example evolutionary development of a reliable communication system requires a substantial amount of altruism and it is not clear whether standard explanations that refer to kin selection or reciprocal altruism are applicable (for example kin selection does not explain our willingness to talk to non-kin). Another problem is concerned with the interaction of evolution and learning, sometimes known as a Baldwin effect. In some cases, learning is known to direct the evolutionary changes, and perhaps in such a way humans developed a language-specific adaptations commonly termed Language Acquisition Device (LAD). Efficiency of the Baldwin effect and even the very existence of LAD remain, however, open problems. There is perhaps a little chance that computational modelling will definitely resolve these issues. But already at the level of constructing appropriate models one has to quantify relevant processes and effects, and even that can provide a valuable insight.

1.6.1. *Evolution and language development*

The ability to use language distinguishes humans from all other species. Certain species also developed some communication modes but of much smaller capabilities as well as complexity. Since several decades various schools are trying to explain the emergence and development of language. Nativists argue that langauge capacity is a collection of domain-specific cognitive skills that are somehow encoded in our genome. However, the idea of the existence of such a Language Acquisition Device or "language organ" (the term coined by their most prominent representative Noam Chomsky[13]), was challenged by empiricists, who argue that linguistic performance of humans can be explained using domain-general learning techniques. The recent critique along this line was made by Sampson,[89] who questions even the most appealing argument of nativists, that refer to the poverty of stimulus and apparently fast learning of grammar by children. An important issue of possible adaptative merits of language does not seem to be settled either. Non-adaptationists, again with Chomsky as the most famous representative,[14] consider language as a side effect of other skills and thus claim that its evolution, at least at the beginning, was not related with any fitness advantage. A chief argument against the non-adaptationist stand is

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the observation that there is a number of costly adaptations that seem to support human linguistic abilities such as a large brain, a longer infancy period or descended larynx. Recently, in their influential paper, Pinker and Bloom argued that, similarly to other complex adaptations, language evolution can only be explained by means of natural selection mechanisms.[79] Their paper triggered a number of works where language was examined from the perspective of evolutionary biology or game theory.[42,46] In particular, Nowak et al. used some optimization arguments, that might explain the origin of some linguistic universals.[71,72] They suggest that words appeared in order to increase the expressive capacity and sentences (made of words) limit memory requirements. Confrontation of nativists with empiricists and adaptationists with non-adaptationists so far does not seem to lead to consensus but certainly deepened our understanding of these problems.[97]

Recently, a lot of works on the language emergence seem to have an evolutionary flavour. Such an approach puts some constraints on possible theories of the language origin. In particular, it rules out non-adaptationist theories, where language is a mere by-product of having a large and complex brain.[31] The emergence of language has been also listed as one of the major transitions in the evolution of life on Earth.[61] An interesting question is whether this transition was variation or selection limited.[105] In variation limited transitions the required configuration of genes is highly unlikely and it takes a considerable amount of time for the nature to invent it. For selection limited transitions the required configuration is easy to invent but there is no (or only very weak) evolutionary pressure that would favour it. Relatively large cognitive capacities of primates and their genetic proximity with humans suggests that some other species could have been also capable to develop language-like communication. Since they did not, it was perhaps due to a weak selective pressure. Such indirect arguments suggest that the emergence of language was selection limited.[105]

Some interesting results can be obtained by applying game-theory reasoning to one of the most basic problems of emerging linguistic communication, namely why do we talk (at all!) and why do we exchange valuable and trustful information. Since speaking is costly (it takes time, energy and sometimes might expose a speaker to predators), and listening is not, such a situation seems to favour selfish individuals that would only listen but would not speak. Moreover, in the case of the conflict of interests the emerging communication system would be prone to misinformation or lying. The resolution of these dilemmas usually refers to the kin selec-

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tion[34] or reciprocal altruism.[108] In other words, speakers remain honest
because they are helping their relatives or they expect that others will do
the same for them in the future. As an alternative explanation Dessalles[23]
suggests that honest information is given freely because it is profitable - it
is a way of competing for status within a group. Computational modelling
of Hurford[41] gives further evidence that speaking might be more profitable
than listening. Hurford considered agents engaged in communicative tasks
(one speaker and one hearer) and their abilities evolved with the genetic
algorithm that was set to prefer either communicative or interpretative suc-
cess. Only in the former case the emerging language was similar to natural
languages were synonymy was rare and homonymy tolerated. When in-
terpretative success was used as the basis of selection then the converse
situation (unknown in natural language) arose: homonymy was rare and
synonymy tolerated. Some related results on computational modelling of
the honest cost-free communication are reported by Noble.[70]

A necessary ingredient of language communication is learning. It is
thus legitimate to ask whether darwinian selection might be responsible
for the genetic hard-wiring of a Language Acquisition Device. Indeed, this
(to some extent hypothetical) organ is most likely responsible for some of
the arbitrary (as opposed to the functional) linguistic structures. But for
such an organ to be of any value, an individual first has to acquire the
language. The inheritance of characteristics acquired during an individual
lifetime is usually associated with discredited lamarckian mechanism and
thus considered to be suspicious. However, the relation between evolution
and learning is more delicate and the attempts to clarify the mutual inter-
actions of these two adaptive mechanisms have a long history. According
to a purely darwinian explanation, known as a Baldwin effect[7,96,114], there
might appear a selective pressure in a population for the evolution of the
instinctive behaviour that would replace the beneficial, but costly, learned
behaviour.[109] Baldwin effect presumably played an important role in the
emergence and evolution of language but certain aspects of these processes
still remain unresolved.[115] For example, one of the assumptions that is
needed for the Baldwin effect to be effective is a relatively stable environ-
ment since otherwise rather slow evolutionary processes will not catch up
with the fast changing environment. Since the language formation processes
are rather fast (in comparison to the evolutionary time scale), Christiansen
and Chater questioned the role of adaptive evolutionary processes in the
formation of arbitrary structures like Language Acquisition Device.[16] Ac-
tually, they suggest a much different scenario, where it is a language that

adapted to human brain structures rather than vice versa.

1.6.2. *Language as a complex adapting system*

From the above description it is clear that studying of the emergence and
evolution of language is a complex and multidisciplinary task and requires
cooperation of not only linguists, neuroscientists, and anthropologists, but
also experts in artificial intelligence, computer sciences or evolutionary bi-
ology.[73] One can distinguish two levels at which language can be studied
and described[22] (Fig. 1.6). At the individual level the description centers
on the individual language users: their linguistic performance, language ac-
quisition, speech errors, speech pathologies or brain functioning in relation
with language processing. At the individual level the language of each in-
dividual is slightly different. Nevertheless, within certain population these
individuals can efficiently communicate and that establishes the population
level. At this level the language is considered as an abstract system that
exists in a sense separately from the individuals users. There are numerous
interactions between these two levels. Indeed, the linguistic behaviour of
individuals depends on the language (at the population level) specific to
the population they are part of. And, as a feedback, the language used in a
given population is a collective behaviour and emerges from linguistic be-
haviour of individuals composing this population. Various processes shap-
ing such a complex system are operating at different time scales. The fastest
dynamics is operating at the individual level (ontogenetic timescale[44]) that
includes, for example, language acquisition processes. Much slower pro-
cesses, such as migrations of language populations, dialects formation or
language extinctions, are operating at the so-called glossogenetic timescale.
The slowest processes govern the biological evolution of language users and
that defines the phylogenetic timescale. Processes operating at these dif-
ferent timescales are not independent (Fig. 1.6). Biological evolution might
change linguistic performance of individuals and that might affect the glos-
sogenetic processes. For example, a mutation that changes the vocal ability
of a certain individual, if spread in his/her population, might lead to a di-
alect formation or a language extinction. Such population-level processes
might change the selective pressure that individual language users are ex-
posed to and that might affect phylogenetic processes, closing thus the
interaction loop.

Various levels of descriptions and processes operating at several
timescales suggest that complex models must be used to describe adequately

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the language evolution. Correspondingly, the analysis of such models and predicting their behaviour also seem to be difficult. It is known that some phenomena containing feedback interactions might be described in terms of nonlinear differential equations, such as for example already described Lotka-Volterra equations. The behaviour of such nonlinear equations is often difficult to predict, since abrupt changes even of the qualitative nature of solutions might take place. Language evolution is, however, much more complex than ecological problems of interacting populations and its description in terms of differential equations would be much more complicated if at all feasible. It seems that recently the most promising and frequently used approach to examine such systems is computational modelling of multi-agent systems. Using this method one examines a language that emerges in a bottom-up fashion as a result of interactions within a group of agents equipped with some linguistic functions. Then one considers language as a complex adaptive system that evolves and complexifies according to biologically inspired principles such as selection and self-organization.[102] Thus, the emerging language is not static but evolves in a way that hopefully is similar to human language evolution. Of course, using such an approach one cannot explain all intricacies of human languages. A more modest goal would be to understand some rather basic features that are common to all languages such as meaning-form mappings, origin of linguistic coherence (among agents without central control and global view), or coevolutionary origin of grammar and meaning.

Within such a multi-agent approach, two groups of models can be distinguished. In the first one, originating from the so-called iterated learning model, one is mainly concerned with the transmission of language between successive generations of agents.[11,45] Agents that are classified as teachers produce some expressions that are passed to learners that try to infer their meaning using statistical learning techniques such as neural networks. After a certain number of iterations teachers are replaced by learners and a new population of learners is introduced. The important issue that the iterated learning model has successfully addressed is the transition from holistic (complex meaning expressed by a single form) to compositional language (composite meaning is expressed with composite form). However, since such a procedure is computationally relatively demanding and the number of communicating agents is thus typically very small, the problem of the emergence of linguistic coherence must be neglected in this approach. To tackle this problem Steels introduced a naming game model[101]. In this approach one examines a population of agents trying to establish a common

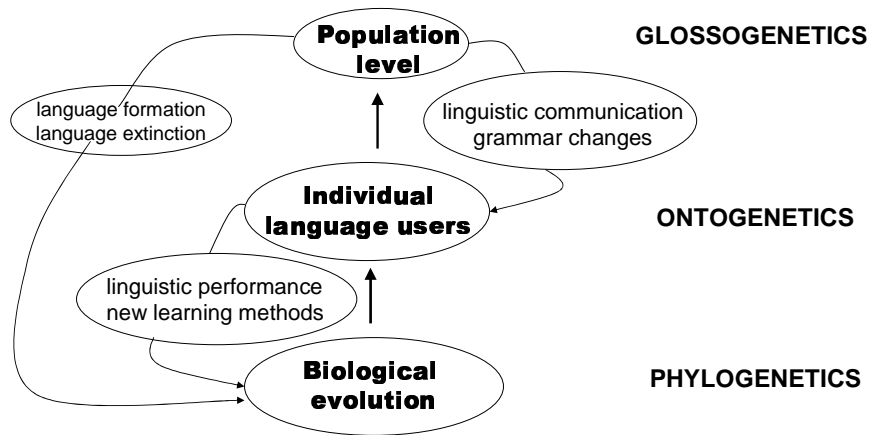Fig. 1.6.   Language as a complex adaptive system.Many different processes governing the language evolution are entangled at various levels. Relatively fast individual level (ontogenetics), comprising e.g., langauge acquisition processes, is determined mainly by interactions between individual language users. Much slower are populational-level processes (glossogenetics) such as language formations, extinctions, grammar changes or migrations. To obtain a complete description one has to consider also biological evolution (phylogenetics) and these are the slowest processes of the language evolution. Various processes at individual and population level affect the fitness landscape and that influences the biological evolution level. Similarly, individual language user level is affected by populational level processes.

vocabulary for a certain number of objects present in their environment. The change of generations is not required in the naming game model since the emergence of a common vocabulary is a consequence of the communication processes between agents, and agents are not divided into teachers and learners but take these roles in turn.

1.6.3.   *Evolutionary naming game*

It seems that the iterated learning model and the naming-game model are at two extremes: the first one emphasizes the generational turnover while the

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latter concentrates on the single-generation (cultural) interactions. Since in the language evolution both aspects are present, it is desirable to examine models that combine evolutionary and cultural processes. Recently we have introduced such a model[55,56] and below we briefly describe it properties.

In our model we consider a set of agents located at sites of the square lattice of the linear size N. Agents are trying to establish a common vocabulary on a single object present in their environment. An assumption that agents communicate only on a single object does not seem to restrict the generality of our considerations and has already been used in some other studies of naming game[8,19] or language-change[67,68] models. A randomly selected agent takes the role of a speaker that communicates a word chosen from its inventory to a hearer that is randomly selected among nearest neighbours of the speaker. The hearer tries to recognize the communicated word, namely it checks whether it has the word in its inventory. A positive or negative result translates into communicative success or failure, respectively. In some versions of the naming game model[8,19] a success means that both agents retain in their inventories only the chosen word, while in the case of failure the hearer adds the communicated word to its inventory.

To implement the learning ability we have modified this rule and assigned weights w_i ($w_i > 0$) to each i-th word in the inventory. The speaker selects then the i-th word with the probability $w_i / \sum_j w_j$ where summation is over all words in its inventory (if its inventory is empty, it creates a word randomly). If the hearer has the word in its inventory, it is recognized. In addition, each agent k is characterized by its learning ability l_k ($0 < l_k < 1$), that is used to modify weights. Namely, in the case of success both speaker and hearer increase the weights of the communicated word by their learning abilities, respectively. In the case of failure the speaker subtracts its learning ability from the weight of the communicated word. If after such a subtraction a weight becomes negative, the corresponding word is removed from the repository. The hearer in the case of failure, i.e., when it does not have the word in its inventory, adds the communicated word to its inventory with a unit weight.

Apart from communication, agents in our model evolve according to the population dynamics: they can reproduce, mutate, and eventually die. To specify intensity of these processes we have introduced the communication probability p. With the probability p the chosen agent becomes a speaker and with the probability $1 - p$ a population update is attempted. During such a move the agent dies with the probability $1 - p_{\text{surv}}$, where $p_{\text{surv}} = \exp(-at)[1 - \exp(-b \sum_j w_j / \langle w \rangle)]$, and $a \sim 0.05$ and $b = 5$ are

certain parameters whose role is to ensure a certain speed of population turnover. Moreover, t is the age of an agent and $\langle w \rangle$ is the average (over agents) sum of weights. Such a formula takes into account both its linguistic performance (the bigger $\sum_j w_j$ the larger p_{surv}) and its age. If the agent survives (it happens with the probability p_{surv}), it breeds, provided that there is an empty site among its neighbouring sites. The offspring typically inherits parent's learning ability and the word from its inventory that has the highest weight. In the offspring's inventory the weight assigned initially to this word equals one. With the small probability p_{mut} a mutation takes place and the learning ability of an offspring is selected randomly anew. With the same probability an independent check is made whether to mutate the inherited word. Numerical simulations show that the described below behaviour of our model is to some extent robust with respect to some modifications of its rules. For example, qualitatively the same behaviour is observed for modified parameters a and b, different form of the survival probability p_{surv} (provided it is a decreasing function of t and an increasing function of $\sum_j w_j$), or different breeding and/or mutation rules. To examine the behaviour of the model we have measured the communication success rate s defined as an average over agents and simulation time of the fraction of successes with respect to all communication attempts. Moreover, we have measured the average learning ability l.

Our model captures all three basic aspects of language: learning, culture, and evolution. Agents in our model are equipped with an evolutionary trait: learning ability. When communication between agents is sufficiently frequent (i.e., when p is large enough), cultural processes create a niche in which a larger learning ability becomes advantageous. It causes an increase of learning ability, but its large value in turn makes the cultural processes more efficient. As a result the model was shown to undergo an abrupt bio-linguistic transition where both linguistic performance (s) and ability (l) of agents change very rapidly (see Figs. 1.7-1.8).[55] It was also shown that under the plausible assumption, that the intensity of communication increases continuously in time, this bio-linguistic transition is replaced with a series of fast, transition-like changes.[56] In our opinion, the proposed model shows that linguistic and biological processes have a strong influence on each other, which has certainly contributed to an explosive development of our species.
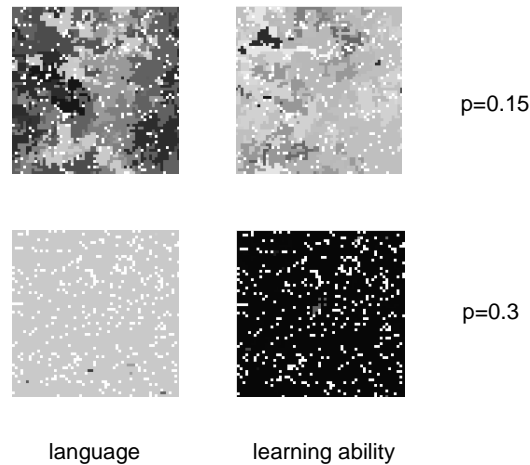
p=0.15

p=0.3

language   learning ability

Fig. 1.7.   Exemplary configurations of the evolutionary naming game model[55,56] with $L = 60$ and $p_{\mathrm{mut}} = 0.001$. In the small-p phase (upper panel) communications are infrequent and agents using the same language (left)or having the same learning abilities (right) form only small clusters. In this phase the communication success rate s and the learning ability l are small (see also Fig. 1.8). The larger the learning ability of an agent the darker are pixels representing it (white: l=0; black: l=1). In the large-p phase (lower panel) frequent communications result in the emergence of the common language. Moreover, almost all agents use the same language and have the same, and large, learning ability.

1.6.4.   *Baldwin effect*

That learning in our model modifies the fitness landscape of a given agent and facilitates the genetic accommodation of learning ability is actually a manifestation of the much debated Baldwin effect. The fact that the success rate s and the learning ability l have a jump at the same value of p shows that communicative and biological ingredients in our model strongly influence each other and that leads to the single and abrupt transition. In our model successful communication requires learning. A new-born agent communicating with some mature agents who already worked out a certain (common in this group) language will increase the weight of a corresponding word. As a result, in its future communications the agent will use mainly this word. In what way such a learning might get coupled with evolutionary traits? The explanation of this phenomenon is known as a Baldwin effect. Although at first sight it looks like a discredited Lamarckian phenomenon, the Baldwin effect is actually purely Darwinian.[38,115]   There are usually
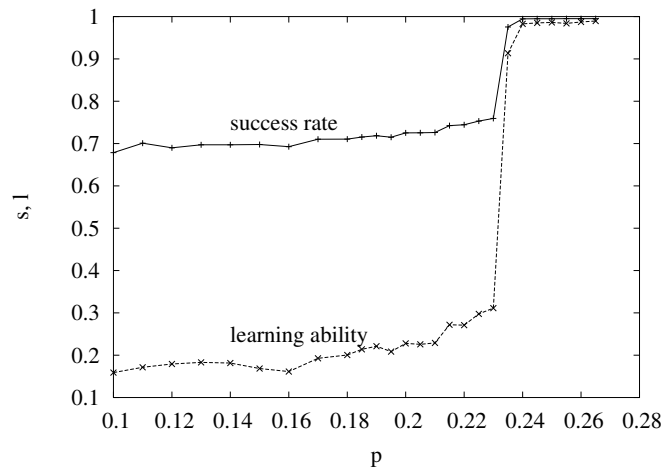
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Fig. 1.8.   The success rate s and the learning ability l as a function of the communication probability p. Calculations were made for system size $L = 60$ and mutation probability $p_{\mathrm{mut}} = 0.001$. Simulation time for each value of p was typically equal to 10^5 steps with $3 \cdot 10^4$ steps discarded for relaxation. A step is defined as a single, on average, update of each site.

some benefits related with the task a given species has to learn and there is a cost of learning this task. One can argue that in such case there is some kind of an evolutionary pressure that favours individuals for which the benefit is larger or the cost is smaller. Then, the evolution will lead to the formation of species where the learned behaviour becomes an innate ability. It should be emphasized that the acquired characteristics are not inherited. What is inherited is the ability to acquire the characteristics (the ability to learn).[109] In the context of the language evolution the importance of the Baldwin effect was suggested by Pinker and Bloom.[79] Perhaps this effect is also at least partially responsible for the formation of the Language Acquisition Device. However, many details concerning the role of the Baldwin effect in the evolution of language remain unclear.[65]

We already argued,[55] that in our model the Baldwin effect is also at work. Let us consider a population of agents with the communication probability p below the threshold value ($p = p_c \approx 0.23$). In such a case the learning ability remains at a rather low level (since clusters of agents using

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the same language are small, it does not pay off to be good at learning the language of your neighbours). Now, let us increase the value of p above the threshold value. More frequent communication changes the behaviour dramatically. Apparently, clusters of agents using the same language are now sufficiently large and it pays off to have a large learning ability because that increases the success rate and thus the survival probability p_{surv}. Let us notice that p_{surv} of an agent depends on its linguistic performance ($\sum_j w_j$) rather than its learning ability. Thus clusters of agents of good linguistic performance (learned behaviour) can be considered as niches that direct the evolution by favouring agents with large learning abilities, which is precisely the Baldwin effect. It should be noticed that linguistic interactions between agents (whose rate is set by the probability p) are typically much faster than evolutionary changes (set by p_{mut}) and such an effect was also observed in simulations.[55]

As a result of a positive feedback (large learning ability enhances communication that enlarges clusters that favours even more the increased learning ability) a discontinuous transition takes place both with respect to the success rate and learning ability . An interesting question is whether such a behaviour is of any relevance in the context of human evolution. It is obvious that development of language, which probably took place somewhere around 10^5 years ago, was accompanied by important anatomical changes such as fixation of the so-called speech gene (FOXP2), descended larynx or enlargement of brain.[39] Linguistic and other cultural interactions that were already emerging in early hominid populations were certainly shaping the fitness landscape and that could direct the evolution of our ancestors via the Baldwin effect.

The examined model is not very demanding computationally. It seems to be possible to consider agents talking on more than one object,[57] or to examine statistical properties of simulated languages such as for example, distributions of their lifetimes or of the number of users. It would be interesting to examine the role of topology of interaction network and place agents on complex networks, like e.g., scale-free networks, that are known to provide a more realistic description of human linguistic interactions.[19] One can also study diffusion of languages, the role of geographical barriers,[76] or formation of language families. There is already an extensive literature documenting linguistic data as well as various computational approaches modelling, for example, competition between already existing natural languages .[1,74,94] The dynamics of the present model, that is based on an act of elementary communication, offers perhaps more natural description

of dynamics of languages than some other approaches that often use some kind of coarse-grained dynamics.

1.7. Conclusions

In the present paper we reviewed computational methods that are used for modelling evolutionary systems. We emphasized the need and advantages of using models with individual-based dynamics. We also drew attention to various time scales of processes that shape the evolution of complex systems. In ecosystems these are ecological and evolutionary time scales. In the language evolution cultural processes set an additional timescale. Perhaps the most interesting phenomena arise from interactions of processes of various times scales. Evolutionary cycling or Baldwin effect are excellent examples of such phenomena, to claim however their satisfactory understanding, much remains to be done.

This mini-review is of course biased by our own experience in this field. We did not even mention about a number of other approaches and techniques of modelling evolutionary systems. Some of them are covered in other chapters of this volume.

Acknowledgements

References

1. Abrams, D. and Strogatz, S. H., (2003). Modelling the dynamics of language death. *Nature* **424**, p. 900.
2. Abramson, G. (1997). Ecological model of extinctions. *Phys. Rev. E* **55**, pp. 785-788.
3. Alroy, J., (1998). Cope's Rule and the Dynamics of Body Mass Evolution in North American Fossil Mammals. *Science* **280**, pp. 731–734.
4. Amaral, L. A. N. and Meyer, M. (1999). Environmental changes, coextinction, and patterns in the fossil record, *Phys. Rev. Lett.* **82**, pp. 652-655.
5. Antal, T. and Droz, M. (2001). Phase transitions and oscillations in a lattice prey-predator model. *Phys. Rev. E* **63** p.056119.

32   *A. Lipowski and D. Lipowska*

6. Bak, P. and Sneppen, K. (1993), Punctuated equilibrium and criticality in a
    simple model of evolution, *Phys. Rev. Lett.* **71**, pp. 4083–4086.
7. Baldwin, J. M. (1896). A new factor in evolution. *American Naturalist* **30**,
    pp. 441-451.
8. Baronchelli, A., Felici, M., Loreto, V., Caglioti, E., and Steels, L.,
    (2006). Sharp transition towards shared vocabularies in multi-agent systems.
    J. Stat. Mech. **P06014**.
9. Blasius, B., Huppert, A., and Stone, L. (1999). Complex dynamics and phase
    synchronization in spatially extended ecological systems. *Nature* **399** pp. 354–
    359.
10. Boccara, N., Roblin, O., and Roger, M. (1994). Automata network predator-
    prey model with pursuit and evasion. *Phys. Rev. E* **50**, pp. 4531–4541.
11. Brighton, H., (2002). Compositional Syntax from Cultural Transmission. *Ar-
    tif. Life* **8**, pp. 25–54.
12. Caldarelli, G., Higgs, P. G., and McKane, A. J. (1998). Modelling coevolution
    in multispecies communities. *J. Theor. Biol.* **193**, pp. 345-358.
13. Chomsky, N., (1965). *Aspects of the theory of syntax*, (Cambridge, MA: MIT
    Press).
14. Chomsky, N., (1972). *Language and Mind*, (San Diego, Harcourt Brace Jo-
    vanovich).
15. Chowdhury, D., Stauffer, D., and Kunwar, A. (2003). Unification of Small
    and Large Time Scales for Biological Evolution: Deviations from Power Law.
    Phys. Rev. Lett. **90**, p.068101.
16. Christiansen M. H. and Chater, N., (2007). *Language as shaped by the brain*,
    preprint.
17. Christiansen, M. H. and Kirby, S. (2003). Language Evolution: The Hardest
    Problem in Science. In Christiansen, M. H. and Kirby, S. (eds.) *Language
    Evolution* (Oxford University Press Inc., New York).
18. Coppex, F., Droz, M., and Lipowski, A., (2004). Extinction dynamics of
    Lotka-Volterra ecosystems on evolving networks, *Phys. Rev. E* **69**, p. 061901.
19. Dall'Asta, L., Baronchelli, A., Barrat, A., and Loreto, V., (2006). Nonequi-
    librium dynamics of language games on complex networks. *Phys. Rev. E* **74**,
    pp. 036105.
20. Davis, M., Hut, P., and Muller, R. M., (1984). Extinction of species by
    periodic comet showers. *Nature* **308**, pp. 715–717.
21. Dawkins, R. (1976). *The Selfish Gene*, (Oxford University Press).
22. de Boer, B., (2006). *Computer modelling as a tool for understanding lan-
    guage evolution.* In *Evolutionary Epistemology, Language and Culture - A non-
    adaptationist system theoretical approach*, Gonthier et al. (eds.) (Dordrecht:
    Springer).
23. Dessalles, J. L., (1998). In J. R. Hurford, J. R. et al. (eds.), *Approaches to
    the Evolution of Language: Social and Cognitive Bases* (Cambridge University
    Press, Cambridge).
24. Dieckmann, U., Marrow, P., and Law, R., (1995). Evolutionary Cycling in
    Predator-Prey Interactions: Population Dynamics and the Red Queen. *J.
    Theor. Biol.* **176**, pp. 91–102.

Computational modelling of evolutionary systems   33

25. Eldredge, N. and Gould, S. J. (1972). Punctuated Equilibria: An Alternative to Phyletic Gradualism. In Schopf, T. J. M. (eds). *Models in Palaeobiology* (Freeman, Cooper, San Francisco) pp. 82-115.

26. Engen, S. and Sæther, B.-E. (2005). Generalizations of the Moran Effect Explaining Spatial Synchrony in Population Fluctuations. *Amer. Natur.* **166**, pp. 603–612,

27. Fox, W. T., (1987). Harmonic analysis of periodic extinctions. *Paleobiology* **13**, pp. 257–271.

28. Fussmann, G. F., Ellner, S. P., and Hairston Jr., N. G. (2003). Evolution as a critical component of plankton dynamics. *Proc. Roy. Soc. B* **270**, pp. 1015–1022.

29. Gang, H., Ditzinger, T., Ning, C. Z., and Haken, H. (1993). Stochastic Resonance without external periodic Force. *Phys. Rev. Lett.* **71**, pp. 807–810.

30. Gingerich, P. D., (1983). Rates of evolution: effects of time and temporal scaling. *Science* **222**, pp. 159-161.

31. Gould, S. J. and Lewontin, R. C. (1979). The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. *Proc. Roy. Soc. London B* **205**, pp 581-598.

32. Grassberger, P. and de la Torre, A. (1979). Reggeon field theory (Schlögls first model) on a lattice; Monte Carlo calculations of critical behaviour, *Ann. Phys. (N.Y.)* **122**, pp. 373-396.

33. Grinstein, G., Mukamel, D., Seidin, R., and Bennett, Ch. H. (1993). Temporally periodic phases and kinetic roughening. *Phys. Rev. Lett.* **70**, pp. 3607–3610.

34. Hamilton, W. D., (1964). The genetical theory of social behaviour (I and II). *J. Theor. Biol.* **7**, pp. 1–16.

35. Hardin, D. P., Takac, P., and Webb, G. F. (1990). Dispersion population models discrete in time and continuous in space. *J. Math. Biol.* **28** pp. 1–20.

36. Hassell, M. P., Comins, H. N., and May, R. M. (1991). Spatial structure and chaos in insect population dynamics. *Nature, Lond.* **353**, pp. 255-258.

37. Hinrichsen, H., (2000). Nonequilibrium Critical Phenomena and Phase Transitions into Absorbing States. *Adv.Phys.* **49** pp. 815-958

38. Hinton, G. and Nowlan, S. (1987). How learning can guide evolution. *Complex Systems* **1**, 495-502.

39. Holden, C., (2004). The origin of Speech. *Science* **303**, pp. 1316-1319.

40. Holmes, E. E., Lewis, M. A., Banks, J., and Veit, R. R. (1994). Partial differential equations in ecology: spatial interactions and populations dynamics. *Ecology* **75**, pp. 17-29.

41. Hurford, J. R., (2003). Why synonymy is rare: Fitness is in the speaker. In Banzhaf, W., Christaller, T., Dittrich, P., Kim, J. T., and Ziegler, J. (eds.), *Advances in artificial life - Proceedings of the 7th European Conference on Artificial Life (ECAL), lecture notes in artificial intelligence*, vol. **2801**, pp. 442-451 (Berlin: Springer Verlag).

42. Jackendoff, R. S., (1992). *Languages of the mind*, (MIT Press).

43. Khibnik and Kondrashov (1997), Three mechanisms of the Red Queen dynamics, *Proc. R. Soc. Lond. B* **264**, pp. 1049-1056.

34   *A. Lipowski and D. Lipowska*

44. Kirby, S., (2002). Natural Language from Artificial Life. *Artif. Life* **8**, pp. 185–215.

45. Kirby, S. and Hurford, J., (2001). *The emergence of Linguistic Structure; An Overview of the Iterated Learning Model*, In *Simulating the Evolution of Language*, Cangelosi, A. and Parisi, D. (eds.) (Springer-Verlag, Berlin).

46. Knight, C., et al. (eds.) (2000). *The Evolutionary Emergence of Language Social Function and the Origin of Linguistic Form*, (Cambridge University Press).

47. Kowalik, M., Lipowski, A., and Ferreira, A. L. (2002). Oscillations and dynamics in a two-dimensional prey-predator system. *Phys. Rev. E* **66**, pp. 066107-1–066107-5.

48. Kowalik, M. (2003). Badanie oscylacji czasowych w układach makroskopowych. PhD. thesis, Adam Mickiewicz University, Poznań Poland (in Polish).

49. Lipowski, A. (1999). Oscillatory behaviour in a lattice prey-predator system. *Phys. Rev. E* **60**, pp. 5179–5184.

50. Lipowski, A., (2000). Multiplicity of species in some replicative systems, *Phys. Rev. E* **61**, pp. 3009–3014.

51. Lipowski, A. (2005). Periodicity of mass extinctions without an extraterrestrial cause. *Phys. Rev. E* **71**, pp. 052902–052905.

52. Lipowski A. and Droz, M. (2002). Phase transitions in nonequilibrium d-dimensional models with q absorbing states. *Phys. Rev. E* **65**, pp. 056114-1 – 056114-7.

53. Lipowski A. and Lipowska, D. (2000). Nonequilibrium phase transition in a prey-predator system. *Physica A* **276**, pp. 456–464.

54. Lipowski A. and Lipowska, D. (2006). Long-term evolution of an ecosystem with spontaneous periodicity of mass extinctions. *Theory in Biosciences* **125**, pp. 67–77.

55. A. Lipowski and Lipowska, D. (2008). Bio-linguistic transition and the Baldwin effect in the evolutionary naming game model. *Int. J. Mod. Phys. C* **19**, pp. 399–407.

56. A. Lipowski and Lipowska, D. (2008). Computational approach to the emergence and evolution of language - evolutionary naming game model. E-print: arXiv:0801.1658.

57. A. Lipowski and Lipowska, D. (2008). Homonyms and synonyms in the n–object naming game model. E-print: arXiv:0810.3442.

58. Lotka, A. J. (1920). Analytical Note on Certain Rhythmic Relations in Organic Systems. *Proc. Natl. Acad. Sci. USA* **6**, pp. 410–415.

59. Matsuda, H., Ogita, N., Sasaki, A., and Sato, K. (1992). Statistical mechanics of population: the Lotka-Volterra model. *Prog. Theor. Phys.* **88**, pp. 1035-1049.

60. May, R. (1972). Limit Cycles in Predator-Prey Communities. *Science* **177**, pp. 900-902.

61. Maynard-Smith, J. and Szathmáry, E. (1997). *The Major Transitions in Evolution* (Oxford University Press, New York).

62. Miller, A. I. and Foote, M., (2003). Increased Longevities of Post-Paleozoic Marine Genera After Mass Extinctions. *Science* **302**, pp. 1030–1032.

63. Mobilia, M., Georgiev, I. T., and Taüber U. C. (2005). Fluctuations and Correlations in Lattice Models for Predator-Prey Interaction. *Phys. Rev. E* **73**, p. 040903.
64. Monetti, R., Rozenfeld, A. F. and Albano, E. F. (2000). Study of interacting particle systems: the transition to the oscillatory behavior of a prey-predator model. *Physica A* **283**, pp. 52–58.
65. Munroe, S. and Cangelosi, A. (2002). Learning and the evolution of language: the role of cultural variation and learning cost in the Baldwin Effect. Artif. Life **8**, pp. 311-339.
66. Murray, J. D. (2002). *Mathematical Biology Vols. I/II* (Springer-Verlag, New York).
67. Nettle, D., (1999). Using Social Impact Theory to simulate language change. *Lingua* **108**, pp. 95–117.
68. Nettle, D., (1999). Is the rate of linguistic change constant? *Lingua* **108**, pp. 119–136.
69. Newman, M. E. J. and Palmer, R. G. (2003). *Modelling Extinction* (Oxford University Press, New York).
70. Noble, J., (2000). In *Evolutionary Emergence of Language*, Knight, C. et al. (eds.) (Cambridge University Press).
71. Nowak, M. A. and Komarova, N. L., (2001). Towards an evolutionary theory of language. *Trends in Cogn. Sci.* **5**, pp. 288–295.
72. Nowak, M. A. and Krakauer, D. C., (1999). The evolution of language. *Proc. Natl. Acad. Sci. USA* **96**, pp. 8028–8033.
73. Nowak, M. A., Komarova, N. L., and Niyogi, P. (2002). Computational and evolutionary aspects of language. *Nature* **417**, pp. 611–617.
74. de Oliveira, P. M. C., Stauffer, D., Wichmann, S., and de Oliveira, S. M., (2007). A computer simulation of language families. E-print:arXiv:0709.0868.
75. Orgel, L. E., (1992). Molecular replication, *Nature* **358**, pp. 203–209.
76. Patriarca, M. and Heinsalu, E. (2008). Influence of geography on language evolution. *Physica A* (in press).
77. Patterson, C. and Smith, A. B. (1989). Periodicity in extinction: the role of the systematics. *Ecology* **70**, pp. 802–811.
78. Pękalski, A. (2004). A short guide to predator-prey lattice models. *Computing in Science and Engineering* **6**, pp. 62–66.
79. Pinker, S. and Bloom, P., (1990). Natural language and natural selection. *Behav. Brain Sci.* **13**, pp. 707–784.
80. Plotnick, R. E., and McKinney, M. L., (1993). Ecosystem organization and extinction dynamics. *Palaios* **8**, pp. 202–212.
81. Plotnick, R. E. and Sepkoski, J. J., (2001). A multiplicative multifractal model for originations and extinctions. *Paleobiology* **27**, pp. 126–139.
82. Prokoph, A., Fowler, A. D., and Patterson, R. T., (2000). Evidence for periodicity and nonlinearity in a high-resolution fossil record of long-term evolution. *Geology* **28**, pp. 867–870.
83. Provata, A., Nicolis, G., and Baras, F. (1999). Ocillatory Dynamics in Low Dimensional Lattices: A Lattice Lotka-Volterra Model. *J. Chem. Phys.* **110**, pp. 8361–8368.

36   *A. Lipowski and D. Lipowska*

84. Rai, R. and Singh, H. (2000). Stochastic resonance without an external peri-
     odic drive in a simple prey-predator model. *Phys. Rev. E* **62**, pp. 8804–8807.
85. Rampino, M. R. and Stothers, R. B., (1984). Terrestrial mass extinctions,
     cometary impacts and the Sun's motion perpendicular to the galactic plane.
     Nature **308**, pp. 709–712.
86. Raup, D. M. and Sepkoski, J. J. (1984). Periodicities of extinctions in the
     geologic past. *Proc. Natl. Acad. Sci. U.S.A.* **81** pp. 801–805.
87. Rohde, R. A. and Muller, R. A., (2005). Cycles in fossil diversity. *Nature*
     434, pp. 208–210.
88. Rozenfeld, A. F. and Albano, E. V. (2001). Critical and oscillatory behavior
     of a system of smart preys and predators. *Phys. Rev. E* **63**, pp. 061907.
89. Sampson, G., (1997). *Educating Eve: The 'Language Instinct' Debate*, (Cas-
     sell).
90. Satulovsky, J. E. and Tomé, T. (1994). Stochastic lattice gas model for a
     predator-prey system. *Phys. Rev. E* **49**, pp. 5073–5079.
91. Schaaffer, W. (1984). Stretching and folding in lynx fur returns: Evidence
     for a strange attractor in nature. *Am. Nat.* **124**, pp. 798-820.
92. Stauffer, D. (1977). Percolation clusters as teaching aid for Monte Carlo
     simulation and critical exponents. *Am. J. Phys.* **45**, pp. 1001.
93. Stauffer, D. (1979). Scaling theory of percolation clusters. *Phys. Rep.* **54**, pp.
     1.
94. Schulze, C., Stauffer, D., and Wichmann, S., (2008). Birth, survival and
     death of languages by Monte Carlo simulation. Commun. Comp. Phys. **3**, pp.
     271-294.
95. Simpson, G. G. (1983). *Fossils and the history of life*(Scientific American
     Library, New York).
96. Simpson, G. G., (1953). The Baldwin Effect. *Evolution* **7**, pp. 110–117.
97. Smith, K., (2003) The Transmission of Language: models of biological and
     cultural evolution. Ph.D. thesis, (The University of Edinburgh).
98. Solé R. V. and Manrubia, S. C. (1996). Extinction and self-organized criti-
     cality in a model of large-scale evolution. *Phys. Rev. E* **54**, pp. R42-R45.
99. Stanley, S. M, (1973). An explanation for Cope's rule. *Evolution* **27**, pp. 1–26.
100. Stanley, S. M, (1990). Delayed recovery and the spacing of major extinctions.
      Paleobiology **16**, pp. 401–414.
101. Steels, L. (1995). A self-organizing spatial vocabulary. *Artif. Life* **2**, pp.
      319–332.
102. Steels, L., (2002). In *Proceedings of the International Workshop of the Self-
      Organization and Evolution of Social Behaviour*, Hemelrijk, C. and Bonabeau,
      E. (eds.) (University of Zurich, Switzerland).
103. Stothers, R. B., (1986). Periodicity of the Earth's magnetic reversals. *Nature*
      322, pp. 444–446.
104. Stothers, R. B., (1993). Flood basalts and extinction events, *Geophys. Res.
      Lett.* **20**, pp. 1399–1402.
105. Számadó, S. and Szathmáry, E., (2006). Language Evolution: Competing
      Selective Scenarios. *Trends. Ecol. Evol.* **21**, pp. 555.
106. Szathmáry, E., (1999). The origin of the genetic code. *Trends in Genetics*

15, pp. 223–229.

107. Thompson, J. N. (1998). Rapid evolution as an ecological process. *Trends in Ecol. Evol.* **13**, pp. 329–332.

108. Trivers, R. L., (1971).The evolution of reciprocal altruism. *Quart. Rev. Biol.* **46**, pp. 35–57.

109. Turney, P., (1996). *Myths and legends of the Baldwin Effect.* In Fogarty, T. and Venturini, G. (Eds.), Proceedings of the ICML-96 (13th International Conference on Machine Learning, Bari, Italy).

110. Vandevalle, N. and Ausloos, M. (1995). The robustness of self-organized criticality against extinctions in a tree-like model of evolution. *Europhys. Lett.* **32**, pp. 613-618.

111. Van Valkenburgh, B., Wang, X., and Damuth, J., (2004). Cope's Rule, Hypercarnivory, and Extinction in North American Canids. *Science* **306**, pp. 101–104.

112. Verhulst, P. F. (1838). Notice sur la loi que la population poursuit dans son accroissement. *Corresp. Math. Phys.* **10**, pp.113–121.

113. Volterra, V. (1926). Variazioni e fluttuazioni del numero dindividui in specie animali conviventi. *Mem. Accad. Nazionale Lincei*, ser. 6, **2**, pp. 31-112.

114. Weber, B. H. and Depew, D. J. (eds.) (2003). *Evolution and Learning - The Baldwin Effect Reconsidered*, (Cambridge, MA, MIT Press).

115. Yamauchi, H. (2004). *Baldwinian Accounts of Language Evolution.* Ph.D. thesis, University of Edinburgh, Edinburgh, Scotland.